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Effects of diet on the interactions between *Hypogastrura denticulata* Bagnall and *Onychiurus furcifer* Börner in laboratory cultures

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Abstract

Diet has been shown to affect the population dynamics of Collembola in laboratory cultures. However, although several studies have examined competitive relationships in these systems, no one has examined the effects of diet. In this study, the effects of diet and food preference on the outcome of competitive interactions were examined. Food type did not affect the dominance rankings of the species, *Onychiurus furcifer* was always dominant over *Hypogastrura denticulata.* In fact, populations of *H. denticulata* virtually disappeared from all the mixed species cultures except those fed on one of the three test fungi, where densities remained at a low level. We speculate that this reflects a partial change from fungal feeding to predation by *O. furcifer* when presented with some fungal species.

Keywords: Collembola, diet, fungi, competition, laboratory experiments.

Effets de l'alimentation sur les interactions entre Hypogastrura denticulata *Bagnall et* Onychiurus furcifer *Börner en élevage au laboratoire.*

Résumé

Il a été démontré que l'alimentation influence la dynamique des populations de Collemboles en élevage. Pourtant, bien que plusieurs études aient examiné la concurrence entre espèces, on n'a pas, jusqu'ici, évalué les effets de l'alimentation. Dans cette étude, on examine les effets de l'alimentation et du choix alimentaire sur la concurrence interspécifique. Nous avons établi que la nature de l'aliment n'influence pas l'ordre de dominance, *Onychiurus furcifer* étant toujours dominant sur *Hypogastrura denticulata.* En effet, les *H. denticulata* ont disparu de toutes les cultures mixtes sauf celle contenant un des champignons testés, où les effectifs se sont maintenus à un niveau très bas. On suppose que ceci est la conséquence d'un changement partiel de régime alimentaire de *O. furcifer*, de mycophage à prédateur, lorsqu'on lui donne certaines espèces de champignons.

Mots-clés : Collembola, régime alimentaire, champignons, compétition, expérimentation en laboratoire.

INTRODUCTION

Many authors have shown that diet can affect the population dynamics of Collembola in laboratory cultures (e.g. Healy, 1965; Vail, 1965; Mills and Sinha, 1971; Harasymek and Sinha, 1974). In general, these differences reflect the nutrient content of the food, modified, to a certain extent, by food preferences and contamination of the food by toxic substances (Snider, 1971; Booth and Anderson, 1979; Bengtsson *et al.*, 1985*b*; Bengtsson *et al.*, 1983, 1985*a*; Shaw, 1988, Verhoef *et al.*, 1988; Walsh and Bolger, 1990; Klironomos *et al.*, 1992). There have been no studies examining the effect of food type on interactions between Collembola, although Christiansen (1967), Culver (1974) and Longstaff (1976) have shown that temperature and light regimes can affect the outcome of competition between species in laboratory cultures.

In this study, the effects of diet on interactions between two species, *Onychiurus furcifer* Börner and *Hypogastrura denticulata* Bagnall, are examined. The animals were fed on three species of fungi to which they showed different degrees of attraction. Walsh and Bolger (1990) found that a light sterile isolate 4 was favoured over a range of nine species offered in preference tests. *Trichoderma viride* was given a low preference by *O. furcifer* but was favoured by *H. denticulata* and *Oidiodendron griseum*, which was the second most favoured species of *O. furcifer* was given a low preference by *H. denticulata*. and

MATERIALS AND METHODS

"Replacement series" are commonly used to analyse competition between species (de Wit, 1960). However, these may be of limited value because they are based on comparisons between actual and expected performance which presumes that competition between species is shared by the two competitors, and cannot distinguish between intra and inter-specific competition (Jolliffe *et al.*, 1984). In these series the proportion of each species differs but the total number of individuals remains the same. Thus, comparisons between single species and mixed cultures are confused because addition of a potential competitor species coincides with a decrease in density of the target species. A design where the number of each species stays the same while the total number changes is more useful. In this design, as the density of each species remains the same, the only difference to the single species cultures is the addition of the second species.

In this study, populations of the two species of Collembola were monitored in four combinations fed on each of three species of fungi. The combinations were monocultures of *O. furcifer* started with 15 animals, monocultures of *H. denticulata* starting with 15 animals, a 15:15 mixture of both species and a 7:7 mixture of both species. The animals used to start the cultures were selected randomly from stock cultures. The fungi used were *Trichoderma viride, Oidiodendron griseum* and a light sterile isolate 4 (Sterile 4). These were cultured in 10 % malt extract medium. Ten replicates of each combination were used. Cultures of Collembola were maintained on a base of plaster of Paris and charcoal in 16 mm diameter vials, at room temperature (15-24 °C). The fungus was presented to the animals on plugs of agar. The animals were fed and watered weekly and counted every second week either from photographs or directly from the cultures.

Cultures started with seven of each species were monitored for thirty-three weeks and those started with fifteen of each species for just ten to fourteen weeks as *H. denticulata* quickly died out in these. Results were analysed using oneway analysis of variance and Duncan's multiple range test.

RESULTS

Growth of individual species populations

In monocultures, populations of *H. denticulata* grew much faster than those of *O. furcifer* fed on the same food (*fig.* 1). Populations feeding on *T. viride* doubled in number by the second week and reached maximum numbers by week 14 with a mean of 114 animals per culture. Those feeding on Sterile 4 began to increase on week 3 and also reached maximum numbers on week

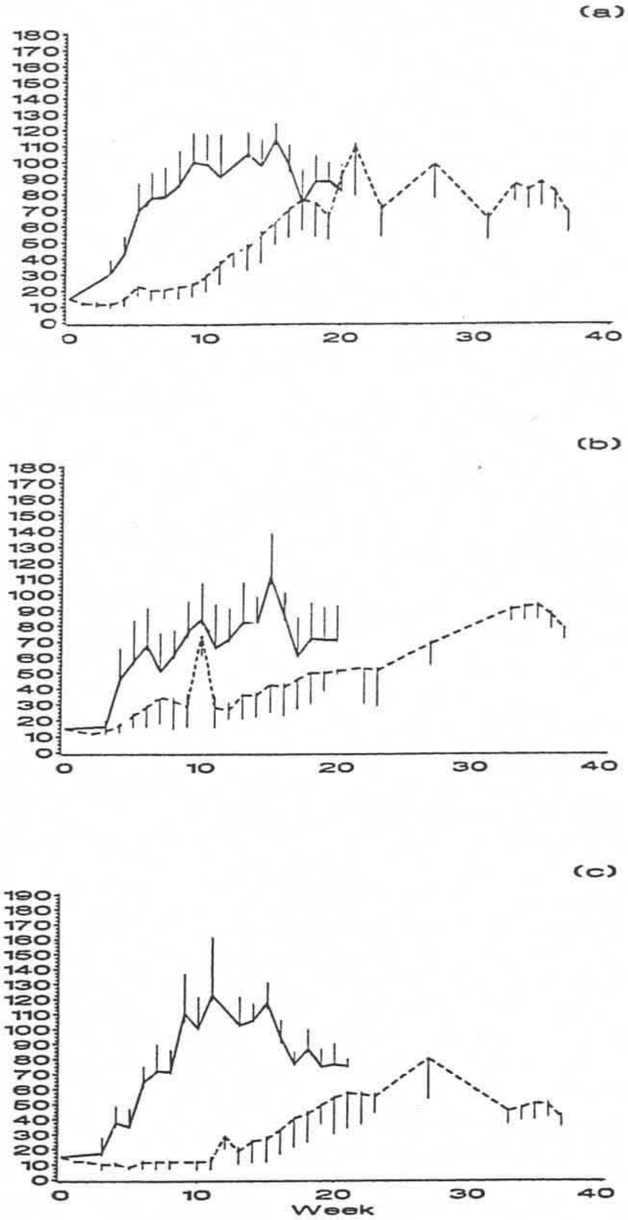

Figure 1. – Average numbers (+ or – s. e.) of *Hypogastrura denticulata* (solid line) and *Onychiurus furcifer* (broken line) in single species cultures fed on (a) *Trichoderma viride* (b) Sterile 4 and (c) *Oidiodendron griseum*.

14 ($\bar{x}$ = 111). A maximum population of 122 animals per culture was reached on week 11 by those feeding on *O. griseum*. In contrast, populations of *O. furcifer* did not start to increase until week 6 and they remained smaller than those of *H. denticulata* until week 16 after which the numbers of *H. denticulata* declined but those of *O. furcifer* continued to grow and reached maximum levels of 110 on *T. viride* (Week 21), 93 on Sterile 4 (Week 35) and 80 on *O. griseum* (Week 27).

In mixed cultures, started with 15 individuals of each species, the opposite was true. Populations of *O. furcifer* increased rapidly to mean values of between 54.1 and 67.7 individual per culture while the populations of *H. denticulata* declined and eventually disappeared (*fig.* 2). In the mixed cultures, started with 7 of each species, the result was similar although populations of *H. denticulata* did not decline to the same extent (*fig.* 3).

Effects of diet on growth of individual species populations

In monocultures, the population growth of *O. furcifer* was affected by diet. When fed on *T. viride*, populations were larger, had faster growth rates and higher fertility. In contrast, *H. denticulata* had similar growth patterns on all three food types. However, in mixed cultures the species of fungus on which the animals fed had significant effects on the population growth of both species.

In cultures started with 15 of each species, populations of *O. furcifer* reached maximum numbers when fed on *O. griseum* reaching 67.7 on week 14. Those fed on Sterile 4 and *T. viride* reached maxima of 40 on week 14 and of 54.1 on week 10 respectively. On weeks 8 and 10 there were significantly more *O. furcifer* in *O. griseum* cultures than in those feeding on Sterile 4. This pattern differed from that observed in the single speices cultures where numbers were never largest on *O. griseum*. In fact, in the final five weeks of the experiment, numbers in monocultures fed on *T. viride* and Sterile 4 were significantly larger than those in *O. griseum* cultures (*fig.* 1).

In the case of *H. denticulata*, significant differences were not observed initially in 15:15 cultures but, on week 12, the numbers in the cultures fed on Sterile 4, were greater than those fed on either of the other species. In later weeks only populations fed on Sterile 4 survived (*fig.* 2).

In the 7:7 cultures, *O. furcifer* achieved similar growth rates when fed on *T. viride* and Sterile 4. Numbers on *T. viride* increased erratically up to a maximum of 49.4 on week 29, those on Sterile 4 reached a mean of 48.9 animals on week 23. As in 15:15 cultures, the highest growth rate was achieved by populations fed *O. griseum*.

Populations of *O. furcifer* differed on only two weeks in the 7:7 cultures and there were no significant

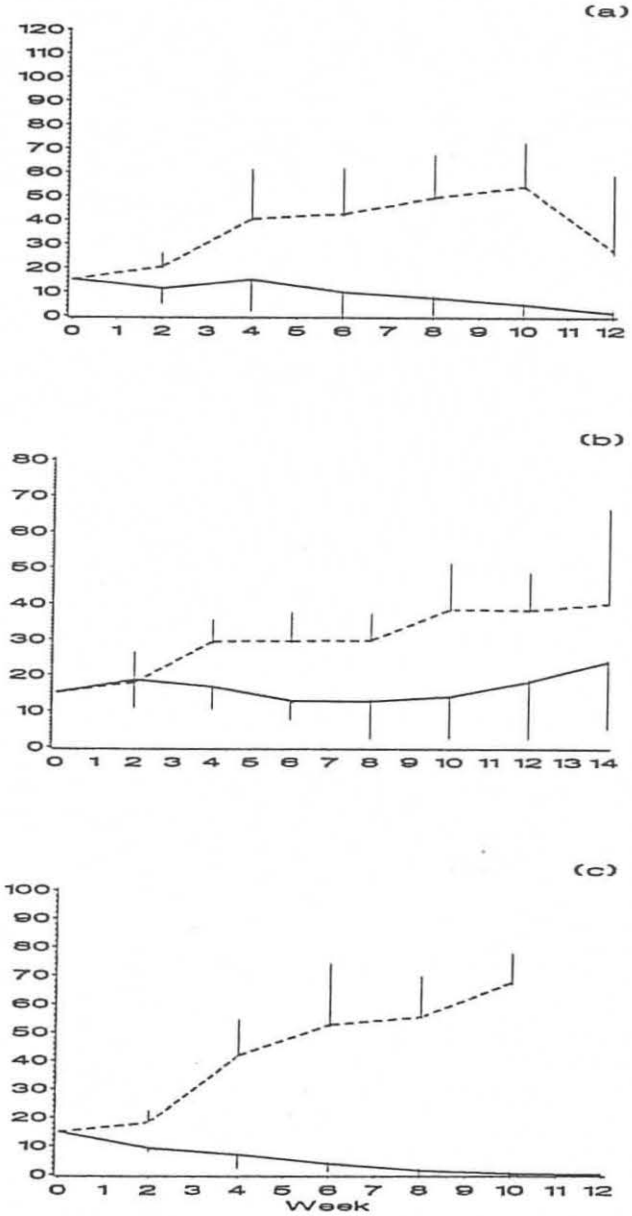

Figure 2. – Average numbers (+ or – s. e.) of *Hypogastrura denticulata* (solid line) and *Onychiurus furcifer* (broken line) in mixed species cultures fed on (a) *Trichoderma viride* (b) Sterile 4 and (c) *Oidiodendron griseum*. Cultures were started with fifteen of each species.

differences in populations of *H. denticulata*. However, although no significant differences could be found between populations of *H. denticulata*, an examination of *figure* 3 suggests that growth is quite different on the three fungal species, being greatest on Sterile 4. The failure to find significant differences may be due to the large number of cultures in which *H. denticulata* died out, e.g. by week 6, six of the *T. viride* cultures contained none of this species, and by week 10 half of the *O. griseum* cultures had no individuals of this species. Another factor may

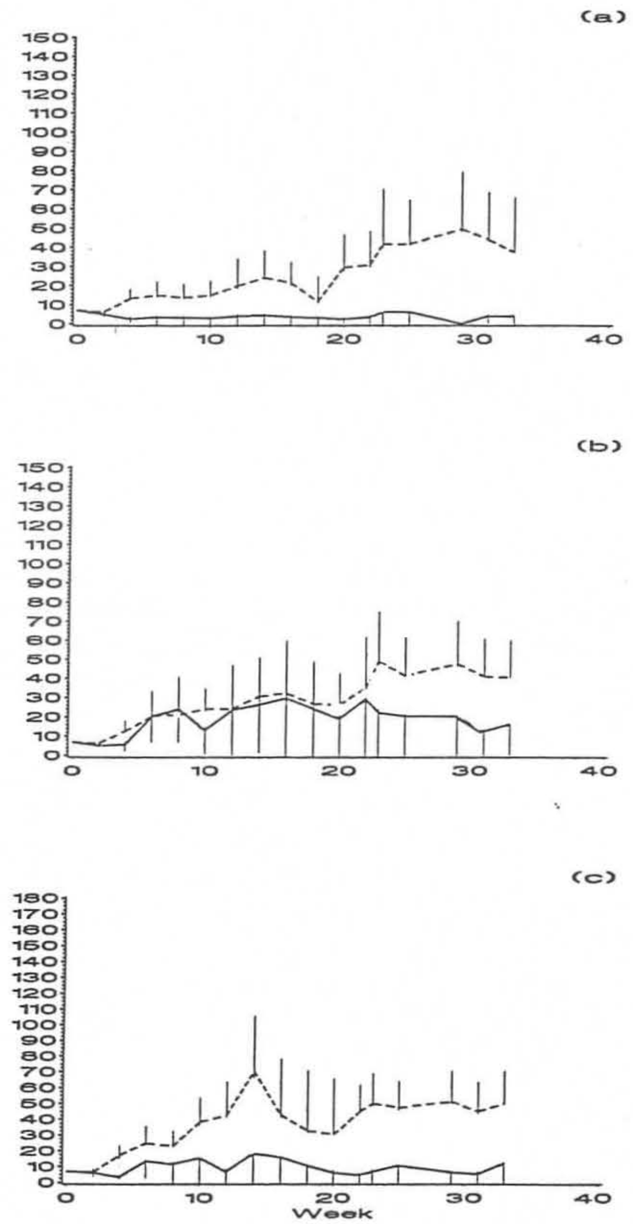

Figure 3. – Average numbers (+ or – s. e.) of *Hypogastrura denticulata* (solid line) and *Onychiurus furcifer* (broken line) in mixed species cultures fed on (a) *Trichoderma viride* (b) Sterile 4 and (c) *Oidiodendron griseum*. Cultures were started with seven of each species.

be the large variations among the populations which survived. On week 4 the variance on *T. viride* was 6.95 compared with a mean value of 3.5, while on Sterile 4 cultures it was more than twice the mean. By week 6, the variance on *T. viride* cultures was eight times the mean, on Sterile 4 cultures it was thirteen times the mean and on *O. griseum* it was seventeen times. A plot of the number of *H. denticulata* against the number of *O. furcifer* for weeks 10, 16 and 31 shows that large numbers of *H. denticulata* only occurred in cultures with small numbers of *O. furcifer* implying competition and/or competitive exclusion (*fig.* 4).

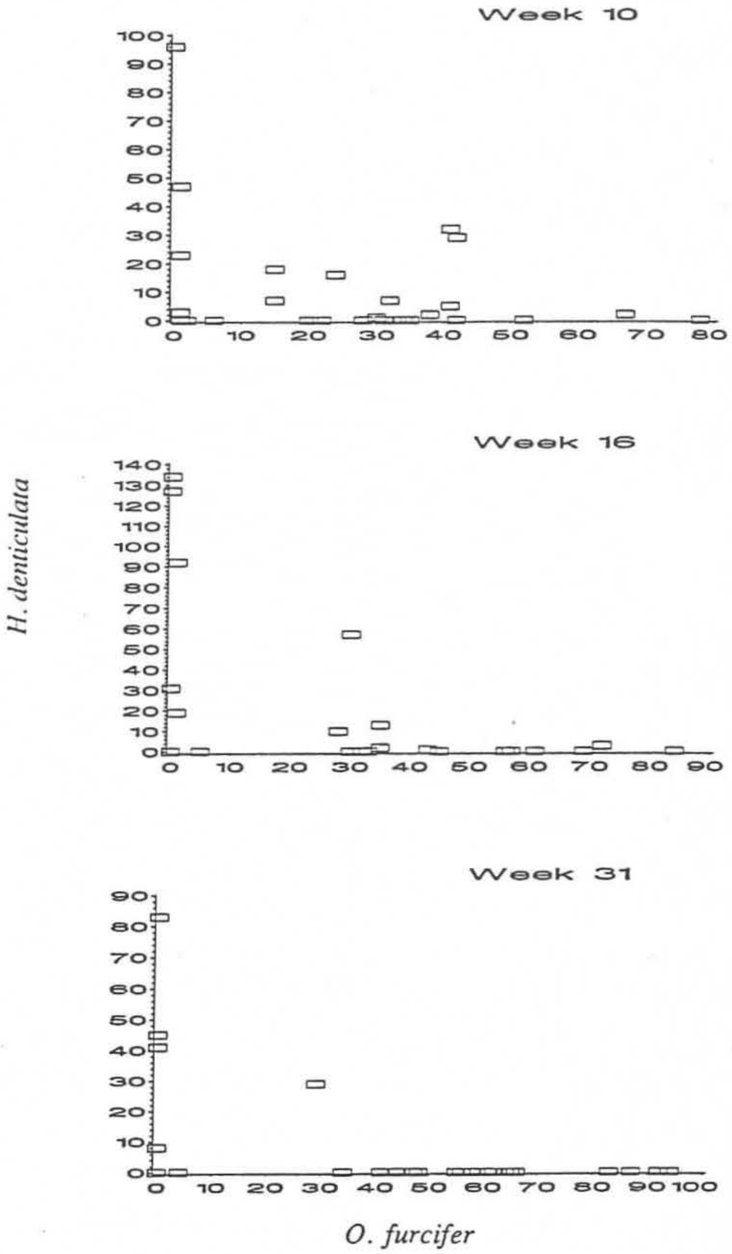

Figure 4. – Relationships between the numbers of *Hypogastrura denticulata* and *Onychiurus furcifer* in cultures started with seven of each species.

Growth of populations in mixed versus mono-species cultures

Populations of *O. furcifer* feeding on *T. viride* and *O. griseum* were larger in 15:15 cultures than in the mono-species cultures on all weeks except one.

However, there were significant differences on only two weeks among the cultures fed with Sterile 4.

The comparison of mono-species cultures with the 7:7 cultures was somewhat more varied as the response of *O. furcifer* to the presence of *H. denticulata* differed with the food source. Populations feeding on *T. viride* were significantly larger in single species cultures on weeks 2, 10-20 and week 33. On the other weeks populations were not significantly different, although the monocultures began with more than double the numbers in the mixed cultures. Populations fed on Sterile 4 were significantly larger in single species cultures on weeks 2, 10 and 33 only. However, animals feeding on *O. griseum* showed the opposite effect. On week 2 there were significantly more animals in single species cultures but in later weeks there were significantly more in the mixed cultures.

Numbers of *H. denticulata* were always significantly greater in monocultures than in mixed cultures.

Comparison between mono-cultures and total in mixed cultures

In most cases there was no significant difference between numbers of *H. denticulata* in mono-cultures and total numbers in the 15:15 cultures. On the weeks where a significant difference was observed, numbers were greater in monocultures. A similar result was observed in the 7:7 cultures. During weeks 2 to 12 the total in 15:15 cultures was greater than in mono-cultures of *O. furcifer* when fed on *O. griseum* and *T. viride*. Those feeding on Sterile 4 were significantly greater in mono-cultures on weeks 2, 4, 12 and 14 but no significant difference was observed on weeks 6, 8 and 10.

Mono-cultures of *O. furcifer* had significantly greater numbers than the total in 7:7 cultures when fed on *T. viride* from weeks 12-20 and week 33. On all other weeks there was no significant difference. Cultures on Sterile 4 were significantly different on 2 weeks. On week 12 total numbers were greater than mono-cultures while on week 33 the opposite was observed. Cultures feeding on *O. griseum* showed similar results in both 7:7 and 15:15 cultures, in all cases where a significant differencee was observed the total number was greater than the number in monocultures.

DISCUSSION

Walsh and Bolger (1990) have shown that diet affects the population dynamics of *O. furcifer* in single species laboratory cultures but were unable to show any effect on the population growth rates of *H. denticulata*. In mixed cultures, the population growth rates of both species were affected by diet. However, in single species cultures, *O. furcifer* performed best when fed with *T. viride* but in mixed cultures the highest growth rates were found in populations fed with *O. griseum*. This suggests that the differences in growth rates must reflect compound effects of diet type and the form of interaction between the Collembola species.

Christiansen (1967) distinguished three types of outcome in studies of direct interactions between collembolan species in laboratory cultures: (i) one species dominates from the start; (ii) the dominant species changes with time and (iii) no dominance is displayed and the species coexist. In the present study, type (i) outcome was demonstrated in all cases except where the animals were fed on Sterile 4 when the outcome was similar to Christiansen's type (iii).

Comparisons of the population sizes in single and mixed species cultures indicate that the presence of *H. denticulata* never led to a reduction in the number of *O. furcifer* present. In fact, the *Onychiurus* populations were actually larger in mixed cultures when fed on *O. griseum*. On the other hand the presence of *Onychiurus* always resulted in reduced numbers of *Hypogastrura* but the level of reduction was very dependent on diet. Populations of *H. denticulata* survived to the end of the experiment in cultures fed on Sterile 4 but declined quickly in the other cultures. It therefore appears that *O. furcifer* is a dominant competitor over *H. denticulata* under the culture conditions used and that the presence of *H. denticulata* can actually benefit *O. furcifer*.

In most studies direct interactions between collembolan species produce negative effects although Christiansen *et al.* (1992) showed that the presence of *Xenylla grisea* had a temporary beneficial effect on populations of *Folsomia candida*. Similarly, Longstaff (1976) found that, under some conditions, the fecundity of *Onychiurus armatus* was increased in the presence of *H. denticulata* and he suggested that *H. denticulata* provided an increase in egg laying sites by chewing up the culture medium and by the deposition of faeces. Christiansen *et al.* (1992) have also shown that airborne chemicals can have positive effects on interacting populations. Either or both of these could also have been operative in the present instance. However, they would not explain the decrease in *H. denticulata* populations in mixed cultures or why the rate of decline varied with diet. The fact that *H. denticulata* populations survived in the cultures fed on the preferred food of *Onychiurus* (Sterile 4) but virtually disappeared when the animals were fed on other species of fungus suggests that *Onychiurus* changed, at least partially, from feeding on fungus to predation when presented with some fungal species. Preliminary observations showed that eggs and young of *Hypogastrura* are apparently consumed in mixed cultures but it was not clear which species ate them. Oophagy has been reported for *Hypogastrura* (Longstaff, 1976) and *Onychiurus* feed on exuviae in culture therefore both could presumably become predatory under certain conditions and have the enzyme complement to digest chitin. In fact, some

species, such as *Folsomia candida* have symbiotic bacteria in their guts which help them digest chitin (Borkott and Insam, 1990) and Saur and Ponge (1988) have demonstrated that a number of species of the Tulbergiinae family digest chitin without the help of symbiotic bacteria. It has also been observed that some species of mite, generally considered to be fungal feeders, also consume nematodes (Walter *et al.*, 1986; Martikainen and Huhta, 1990).

It appears therefore that, under the conditions of the laboratory culture, *O. furcifer* is the dominant competitor. Indeed it has many of the characters of a K-selected species. It has a relatively slow population growth rate, it is a good competitor and makes optimal use of the resources at its disposal by eating its exuviae and faeces. On the other hand, *H. denticulata* appears to be r-selected. It has a relatively high population growth rate, it is a poor competitor and is not as efficient in its use of resources as *Onychiurus*.

There are obvious limitations to laboratory experiments such as those described. The species used may not normally occur together or with the fungi used as food and the climatic conditions may be unrealistic. However, even with these constraints, it is possible to say that, given constant conditions, while Collembola may be unspecialised feeders, food type does exert a strong influence on population dynamics and interspecific interactions and to speculate that the form of interaction may change from assymetric competition, when feeding on preferred food, to predation when less preferred food is offered.

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